PROCEEDINGS
OF THE
NATIONAL ACADEMY OF SCIENCES
Volume 30 July 15, 1944 Number 7
Copyright 1944 by the National Academy of Sciences

X-RAY SENSITIVITY CHANGES IN MEIOTIC CHROMOSOMES AND THE NUCLEIC ACID CYCLE

By A. H. Sparrow*

Biological Laboratories, Harvard University

Communicated May 17, 1944

It is well known that the sensitivity of cells to x-ray injury is influenced by such factors as moisture content, the stage of nuclear or chromosomal development, the percentage of cells in mitosis and the degree of tissue differentiation. However, concerning the change of sensitivity during the nuclear cycle there is much disagreement. Practically all stages have been claimed by one or more authors to be the stage of maximum sensitivity. Resting stage or very early prophase has been claimed to be the most sensitive by Strangeways and Hopwood[1] and by Langendorf and Langendorf.[2] Prophase has been found most sensitive by Marshak,[3,4] Creighton[5] and Sax.[6] Carlson[7] found mid and late prophase most sensitive. Newcombe[8] states that sensitivity increases as the chromosomes approach metaphase while Sax and Swanson[9] have observed that sensitivity decreases during this period. Maximum injury to cells rayed at metaphase is reported by Mottram[10] and by Whiting[11] while Langendorf and Langendorf[2] and Marshak[12,13] claim metaphase and anaphase are least sensitive. Some authors have found two stages of high sensitivity, e.g., metaphase and anaphase by Holthusen,[14] Bozeman[15] and Sparrow,[16] anaphase and prophase by Regaud,[17] anaphase and telophase by Vintemberger[18] and telophase and prophase by Langendorf and Langendorf.[2]

From the results cited above it would appear that maximum sensitivity bears no constant relationship to the stage of mitosis at the time of raying. Yet the general aspects of mitosis and meiosis are remarkably uniform even in very distantly related forms. In the present paper meiotic metaphase and anaphase are shown to be stages of high sensitivity in *Trillium* and a plausible explanation for at least some of the disagreement with the results of other investigators is given. The relationship between nucleic acid concentration and chromosome radiosensitivity is also discussed.

Methods.—Rhizomes of *Trillium erectum* L. were obtained from com-

mercial dealers during October and November. They were kept in a constant temperature room at 6–8°C. except when being examined or rayed. At this temperature meiosis proceeds slowly and a fairly accurate determination of stages is possible. First anaphase is probably the shortest stage but usually lasts at least one day. Meiotic prophase and microspore resting stages are very slow so that several weeks often elapsed between raying and smearing. Low temperature also seemed to reduce the amount of chromosome clumping and stickiness which often follow exposure to x-rays.

All plants were examined by removing part or all of one or more anthers for test smears. It was thus possible to select plants showing a high synchronization of division at the desired stage. This was further aided by the characteristic lack of a regular interkinetic resting nucleus between first and second divisions in this species.[19] The inhibiting effect of x-rays on spindle activity afforded an additional check on the stage rayed. Cells rayed at first metaphase usually developed into tetraploid microspores, those at first anaphase into diploid and those at second anaphase or later into the usual haploid form.

Cells rayed at meiotic prophase were scored for aberrations at first anaphase. Those rayed at metaphase and anaphase showed little or no increase in aberrations until microspore division which followed directly, without an intervening second meiotic division. Scoring was done at microspore metaphase following irradiation at meiotic metaphase and anaphase, and at microspore anaphase following x-ray treatment of microspores in the resting stage.

Results.—The data for doses of 50, 100 and 200 r at various stages of microsporogenesis are given in table 1. In most cases 50 or 100 cells were scored. In two cases (numbers 9 and 10) only 10 cells were counted but in these the very high number of fragments per cell compensates for the relatively small sample. The number of cells actually scored is indicated in table 1 under n but to facilitate comparisons all data have been expressed as the number of aberrations per hundred pollen mother cells.

Chromosomes rayed at first meiotic metaphase and anaphase appear practically normal when examined one, two or three days later. For example, in plant number 10 approximately 9 per cent of 300 first anaphases examined before raying showed a bridge or fragment or both, and when examined two days after exposure to 200 r less than 7 per cent of the cells showed aberrations. Obviously, therefore, the x-rays cause no immediate increase in the percentage of aberrations at first anaphase. However, there is a delayed reaction which becomes apparent in the microspore mitosis. For example, in plant number 9, which was given 200 r at first metaphase, a large number of giant ($4n$) pollen grains were later observed. In these so many fragments were present that it was generally difficult or

impossible to tell which were centric and which were acentric fragments. The mean total of both counted at microspore metaphase was 65.2 ± 7.07. The corresponding mean for diploid microspores resulting from rayed first anaphases was 43.7 ± 3.45 or 87.4 per pollen mother cell. Deducting 20 (the normal microspore chromosome complement derived from each pollen mother cell) gives a corrected mean of 45.2 fragments for each pollen mother cell rayed at first metaphase and 67.4 for each one rayed at first anaphase. The mean number of fragments per pollen mother cell for the same dosage at leptotene-zygotene was 7.48 and 7.87 (plants 7 and 8). Obviously, therefore, the sensitivity of leptotene-zygotene is very much smaller than that of either metaphase or anaphase of the first meiotic division.

TABLE 1

THE NUMBERS OF BRIDGES, RINGS AND FRAGMENTS INDUCED BY RAYING AT DIFFERENT STAGES OF MICROSPOROGENESIS[a]

PLANT NUMBER	STAGE RAYED	DOSE IN r	n[a]	BRIDGES	RINGS	FRAGMENTS	TOTAL ABERRATIONS
1	Leptotene-zygotene	50	100	46	2	117	165
2	Pachytene	50	100	66	1	210	277
3	Leptotene-zygotene	100	50×2	128	2	216	346
4	Late leptotene-zygotene	100	50×2	200	4	580	784
5	Late pachytene	100	50×2	340	6	556	902
6	Microspores (resting stage)	100	100×4	100	8	492	600
7	Leptotene-zygotene	200	50×2	288	16	748	1052
8	Leptotene-zygotene	200	100	230	12	787	1029
9	1st metaphase,	200	10×10	..	[b]	4520	...
10	1st anaphase	200	10×20	..	[b]	6740	...
11	Microspores (resting stage)	200	100×4	256	12	776	1044

[a] Where fewer than 100 pollen mother cells (or the equivalent number of derived microspores) were scored, the data presented have been multiplied by the factor as given under *n*. Thus, the data can be compared directly.

[b] Rings were present but not recorded.

For stages rayed at different dosages the data cannot be compared directly. But since leptotene-zygotene stages were rayed at all dosages, the relative sensitivity at any other stage can be calculated with respect to leptotene-zygotene by assuming that all stages have similar dosage curves. Accordingly, leptotene-zygotene has been assigned an arbitrary unit sensitivity. Then, for any dosage, relative sensitivity is simply the number of aberrations at a given stage divided by the number of aberrations at

leptotene-zygotene for the same dosage. The relative sensitivities given in table 2 are calculated from "total aberrations" in table 1 except for plants 9 and 10. In these calculations were made using fragments only, because scoring was done at microspore metaphase and hence bridges could not be included. The relative sensitivities show an increase from 1 at leptotene-zygotene to 1.7 at pachytene, 2.6 at late pachytene, 5.9 at first metaphase and 8.7 at first anaphase, and then drop again in the post-meiotic resting stage to approximately the same as early meiotic prophase.

TABLE 2

RELATIVE SENSITIVITY OF STAGES BASED ON DATA FROM TABLE 1

STAGE RAYED	RELATIVE SENSITIVITY
Leptotene-zygotene	1.0
Zygotene-early pachytene	2.3
Pachytene	1.7
Later pachytene	2.6
Metaphase I	5.9
Anaphase I	8.7
Microspore resting nucleus (plant no. 6)	1.7
Microspore resting nucleus (plant no. 11)	1.0

Discussion.—A number of recent papers point to the growing recognition of the importance of the nucleic acids in protein synthesis and nuclear metabolism. There is also evidence that small doses of x-rays can temporarily block one or more of the essential processes involved in the nucleic acid cycle.[20] This latter observation has prompted the following discussion of the significance of changes in relative nucleic acid concentrations in terms of chromosomal radiosensitivity.

Relatively small concentrations of desoxyribose nucleic acid are present in resting nuclei while metaphase and anaphase chromosomes contain very high concentrations.[21] Conversely, the high concentration of ribose nucleic acid present in cells undergoing, or about to undergo, rapid proliferation decreases[22, 23, 24] while the desoxyribose content increases.[25, 26] Specifically it has been shown that during meiotic prophase initial high concentrations of ribose nucleic acid fall off[24] and that the desoxyribose, which starts at a low level, increases as metaphase is approached.[26] Presumably the ribose nucleic acid, or ribose nucleotides, pass into the nucleus, are changed into the desoxyribose form, polymerized and incorporated into the structure of the chromosome, probably as nucleohistone.[27, 28] In support of this theory is the recent demonstration by Mitchell[20] that x- and gamma-radiations result in the accumulation of pentose nucleotides in the cytoplasm and inhibit the synthesis of desoxyribose nucleic acid. The inhibition is attributed to enzyme inactivation. Since the ribose nucleotides increase following irradiation and since they may be present in high concen-

trations at stages of low x-ray sensitivity and vice versa, it is clear that their concentration *per se* does not determine high radiosensitivity. For desoxyribose nucleic acid or nucleotides, however, the reverse is true. Stages, such as resting nuclei or early prophase, which have low concentrations of desoxyribose nucleotides or nucleic acid have a low sensitivity, while metaphase and anaphase, stages which have a high concentration, show a high radiosensitivity. This suggests a positive correlation between radiosensitivity and the concentration of desoxyribose nucleic acid or nucleotides. However, it does not necessarily mean that a high content *per se* determines high sensitivity. Other factors may determine high sensitivity and high nucleic acid content may be merely concomitant. This suggestion is in accord with Dale's[29] conclusion that the radiosensitivity of an enzyme can be modified by the amounts and radiosensitivities of other substances present.

Our results indicate that x-rays fail to break metaphase and anaphase chromosomes, as such, but that they somehow react to produce potential breaks which become visible chromatid or chromosome breaks only after the nucleus has passed through an interphase. It has been suggested that nucleic acid protects the metaphase chromosomes from x-ray injury[9, 12, 30] but this now seems improbable. However, the possibility remains that something inherent in the nucleoprotein structure of the chromosome temporarily prevents or inhibits the potential break from becoming a visible one. In this connection it may be significant that following irradiation at metaphase or anaphase breaks appear only after an interphase has occurred during which both the matrix and the nucleic acid structure undergo extensive alterations.

Experimental evidence concerning the physical-chemical changes induced in living cells by x-rays is meager but it is of interest that ultraviolet, which is known to produce qualitative genetic changes similar to those resulting from x-rays can cause a depolymerization of sodium thymonucleate.[31] Since breakdown of the nucleic acid macromolecule has also been suggested as a possible cause of ultra-violet induced mutations[31] it would be of considerable interest to determine whether or not irradiation at metaphase and anaphase would induce more mutations than the same dosage at prophase or resting stage.

Further evidence of the high sensitivity of metaphase is afforded by combined x-ray and colchicine treatments. Guyer and Claus[32] found cancer tissue in rats more sensitive to x-rays after injection of colchicine, and Brücke and Hueber[33] report that skin metastases treated with both colchicine and x-rays completely disappeared while metastases in the same patient not pretreated with colchicine showed a much less favorable response to irradiation. Further, Halberstaedter and Back[34] found that the lethal dose is 50 per cent smaller for Paramoecia which have been pre-

treated with colchicine. Since it is known that colchicine prolongs the metaphase by inhibiting spindle activity, it seems probable that the increased sensitivity to x-rays following colchicine treatment stems from an increase in the percentage of highly sensitive metaphases.

A relationship between malignancy and an abnormally high concentration of desoxyribose nucleic acid (hyperchromatism) has been noted by a number of authors.[35, 36, 37] In plants malignancy in certain types of pollen has also been attributed to abnormal nucleic acid metabolism associated with extra heterochromatic *B*-chromosomes.[38] Since the effectiveness of radiation therapy in cancer is dependent upon differential radiosensitivity it seems plausible that the high radiosensitivity of tumors may be associated with their high content of desoxyribose nucleic acid.

Support of the suggested relationship between desoxyribose nucleic acid and radiosensitivity is afforded by data on break frequency in heterochromatic regions which are characterized by differences in nucleic acid content.[39, 40, 41] White[42] found relatively few x-ray induced breaks in the negatively heterochromatic *X*-chromosome of spermatogonial divisions of *Locusta*, while several authors[43–46] report a significantly higher than random break frequency for positively heterochromatic regions in Drosophila. Since negative and positive heterochromatin are considered to be, respectively, under- and overcharged with desoxyribose nucleic acid with respect to the rest of the chromosomes[27, 41] this is further evidence that sensitivity to x-rays may be related to the concentration of desoxyribose nucleic acid.

From the data presented it seems clear that, in *Trillium*, meiotic metaphase and anaphase are stages of high sensitivity and early meiotic prophase a stage of low sensitivity to x-rays. The prophase to anaphase sensitivity change approaches a 1:9 ratio. Similar ratios have been reported for mitotic divisions in fertilized eggs. Mottram[10] found a 1:8 ratio between resting stage and metaphase in *Ascaris* ova, and Vintemberger[18] a 1:6 ratio between resting stage and telophase in frogs' eggs and a slightly lower value at anaphase. For *Tradescantia*, Sax[47] estimates that meiotic chromosomes are at least ten times as susceptible as those in microspore resting nuclei, but does not identify the meiotic stage of maximum sensitivity. However, metaphase and anaphase are not *generally* recognized as stages of high sensitivity even in recent papers dealing with relative sensitivity.[5, 30, 48–50] Yet evidence for high sensitivity of these stages is available from a remarkalby wide taxonomic range of organisms. These include Protozoa (Paramoecium),[34] Nemathelminthes (*Ascaris*),[10, 14] Insecta (*Sciara* and *Habrobracon*),[15, 11] Amphibia (frog),[18] Mammalia (rat),[32] and in plants the present work on *Trillium*. The observations include both mitotic and meiotic stages. It seems likely, therefore, that metaphase and anaphase stages may prove to be generally of higher sensitivity than prophase and resting stages.

Some of the earlier results are open to question because of the failure to examine the succeeding mitoses. In this connection it is probably significant that all of those who report metaphase or anaphase highly sensitive had examined material at some time after irradiation or used percentage of lethals as a measure of sensitivity. Many who report low sensitivity for these stages made cytological examinations but apparently failed to allow sufficient time between raying and fixation. Dividing cells observed while being irradiated were reported to complete mitosis without showing any adverse effects.[51] Here again it was probably a matter of not continuing observations sufficiently long, for the present investigation indicates that metaphase and anaphase chromosomes, as such, are highly resistant to x-ray breakage but that their high susceptibility to injury is abundantly evident if sought after in the next mitosis. It is therefore concluded that x-ray "hits" on metaphase and anaphase chromosomes do not induce immediate breaks but do induce potential breaks which are not actually realized until the following division. This delay in the appearance of the aberrations is probably responsible for at least some of the controversial claims regarding the radiosensitivity of metaphase and anaphase chromosomes.

Summary.—The relative effect of x-rays on different stages of meiosis and on microspore resting nuclei have been investigated in *Trillium.* Using the number of chromosome aberrations as a measure of sensitivity it was found that sensitivity is low in early meiotic prophase. Pachytene is roughly twice as sensitive, metaphase six and anaphase nine times as sensitive as early meiotic prophase. The sensitivity of post-meiotic resting nuclei is approximately that of early meiotic prophase. Since stages of high sensitivity to x-rays also have a high content of desoxyribose nucleic acid and stages of low sensitivity a low content, it appears that radiosensitivity can be correlated with nucleic acid metabolism. It is also suggested that non-random breaks in heterochromatic regions may be associated with a difference in the amount of desoxyribose nucleic acid in such regions as compared to the adjoining euchromatic chromatin. The relationship of tumor radiosensitivity to nucleic acid content is also briefly discussed.

Acknowledgment.—The author acknowledges financial assistance from The National Research Council and wishes to express his gratitude to Professor Karl Sax for his interest in the problem and reading of the manuscript.

* National Research Fellow 1942–1943.

[1] Strangeways, T. S. P., and Hopwood, F. L., *Proc. Roy. Soc. London*, **B100**, 283–293 (1926).

[2] Langendorf, H., and Langendorf, M., *Strahlentherapie*, **40**, 97–110 (1931).

[3] Marshak, A., *Jour. Gen. Physiol.*, **19**, 179–198 (1935).

[4] Marshak, A., these PROCEEDINGS, **25,** 510–516 (1939).
[5] Creighton, M., *Jour. Exp. Zool.*, **87,** 347–369 (1941).
[6] Sax, Karl, *Genetics*, **25,** 41–68 (1940).
[7] Carlson, J. G., *Jour. Morph.*, **71,** 449–462 (1942).
[8] Newcombe, H. B., *Jour. Genet.*, **43,** 145–171 (1942).
[9] Sax, Karl, and Swanson, C. P., *Amer. Jour. Bot.*, **28,** 52–59 (1941).
[10] Mottram, J. C., *Arch. Middlesex Hospt.*, **30,** 98–119 (1913).
[11] Whiting, A. R., *Jour. Exp. Zool.*, **83,** 249–269 (1940).
[12] Marshak, A., these PROCEEDINGS, **23,** 362–369 (1937).
[13] Marshak, A., *Proc. Soc. Exp. Biol. and Med.*, **38,** 705–713 (1938).
[14] Holthusen, H., *Pfluger's Arch.*, **187,** 1–24 (1921).
[15] Bozeman, M. L., *Genetics*, **28,** 71 (1943).
[16] Sparrow, A. H., *Rec. Genet. Soc. of Amer.*, **12,** 54–55 (1943).
[17] Regaud, C., *Bull. Assoc. franc. Cancer*, **12,** 482–487 (1923).
[18] Vintemberger, P., *Compt. Rend. Soc. Biol.*, **98,** 532–535 (1928).
[19] Sparrow, A. H., Huskins, C. L., and Wilson, G. B., *Can. Jour. Res.*, **C19,** 323–350 (1941).
[20] Mitchell, J. S., *Brit. Jour. Radiology*, **16,** 339–343 (1943).
[21] Caspersson, T., *Skand. Arch. Physiol.*, Suppl. No. 8, **73,** 1–151 (1936).
[22] Caspersson, T., and Thorell, B., *Chromosoma*, **2,** 132–154 (1941).
[23] Mirsky, A. E., in *Recent Advances in Enzymology*, Interscience Publishers, Inc., New York, Vol. 3, pp. 1–34, (1943).
[24] Painter, T. S., *Bot. Gaz.*, **105,** 58–68 (1943).
[25] Brachet, J., *Arch. Biol.*, **44,** 519–576 (1933).
[26] Caspersson, T., *Chromosoma*, **1,** 147–156 (1939).
[27] White, M. J. D., in *Cytology and Cell Physiology*, Oxford University Press, Oxford pp. 139–159, (1942).
[28] Mirsky, A. E., and Pollister, A. W., *Biol. Symposia*, **10,** 247–260 (1943).
[29] Dale, W. M., *Biochem. Jour.*, **36,** 80–85 (1942).
[30] Swanson, C. P., *Jour. Gen. Physiol.*, **26,** 485–494 (1943).
[31] Hollander, A., Greenstein, J. P., and Jenrette, W. V., *Jour. Nat. Cancer Inst.*, **2,** 23–28 (1941).
[32] Guyer, M. F., and Claus, P. E., *Proc. Soc. Exp. Biol. and Med.*, **42,** 565–568 (1939).
[33] Brücke, F. th. v., and Hueber, E. F. v., *Klin. Wchnschr.*, **18,** 1160–1161 (1939).
[34] Halberstaedter, L., and Back, A., *Nature*, **152,** 275–276 (1943).
[35] Biesele, J. J., Poyner, H., and Painter, T. S., *University of Texas Publication*, no. 4243, pp. 1–68 (1942).
[36] Stowell, R. E., *Jour. Nat. Cancer Inst.*, **3,** 111–121 (1942).
[37] Koller, P. C., *Nature*, **151,** 244–246 (1943).
[38] Darlington, C. D., and Thomas, P. T., *Proc. Roy. Soc. London*, **B130,** 127–150 (1941).
[39] Schultz, J., and Caspersson, T., *Arch. f. Exper. Zellforsch.*, **22,** 650–654 (1938).
[40] White, M. J. D., *Jour. Genet.*, **40,** 67–82 (1940).
[41] Darlington, C. D., *Nature*, **149,** 66–69 (1942).
[42] White, M. J. D., *Proc. Roy. Soc. London*, **B119,** 61–84 (1935).
[43] Prokofyeva-Belgovskaya, A. A., *C.R. (Doklady) Acad. Sci. U.R.S.S.*, **23,** 270–272 (1939).
[44] Kaufmann, B. P., these PROCEEDINGS, **25,** 571–577 (1939).
[45] Hinton, T., *Genetics*, **27,** 119–127 (1941).
[46] Muller, H. J., *Cold Spring Harbor Symp. on Quant. Biol.*, **9,** 151–167 (1942).
[47] Sax, Karl, *Genetics*, **23,** 494–516 (1938).
[48] Marshak, A., *Proc. Soc. Exp. Biol. and Med.*, **39,** 194–198 (1938).

[49] Froier, K., Gelin, O., and Gustafsson, A., *Bot. Notiser*, **1941**, 199–216.
[50] Koller, P. C., *Proc. Roy. Soc. Edinburgh*, **B61**, 398–429 (1943).
[51] Canti, R. G., and Donaldson, M., *Proc. Roy. Soc. London*, **B100**, 413–419 (1926).

THE SPORE DISCHARGE MECHANISM OF COMMON FERNS

BY ALLEN L. KING

DEPARTMENT OF PHYSICS, DARTMOUTH COLLEGE

Communicated June 6, 1944

Among ferns the Polypodiaceae are most common and are highly developed. In this family the mature sporangium, rather uniformly, is a flattened obovoid capsule supported on a long pedicel (*P*, Fig. 1). The unicellular thin side walls enclose the region in which spores develop. Along approximately two-thirds of the edge of this lenticular form, a single row of nearly cuboid cells (*A*, Fig. 1) become differentiated. This incomplete ring, the annulus, is prominent on the back and apex of the sporangium and is attached to the pedicel at the rear. From the annulus to the front of the pedicel a number of thin-walled cells complete the ring. Two of these cells meet in a straight line, the stomium (*S*, Fig. 1), and when the sporangium dehisces, cleavage first takes place along this juncture.

The annulus consists of thirteen or more cells with thickened inner and radial walls and thin flexible outer and side walls. The inner walls form a continuous band with crenations due to a slight arching inward at each cell. This band is very elastic and acts as a spring to expel the spores with considerable speed at the time of dehiscence.

When the sporangium becomes mature, evaporation of water from the annular cells induces sufficient stress to cause cleavage at the stomium. The line of cleavage follows cell boundaries toward the rear of the sporangium. Frequently weak lateral cells are split in two.[1] Meanwhile, the annulus slowly straightens and continues to evert sometimes to the extent that the two ends of the recurved annulus almost meet. Nearly all the spores are carried on the free end in a cup formed by the lateral walls of the sporangium. Suddenly the annulus snaps back to its original position and in the process it may catapult spores to distances of 1 to 2 cm.[2]

Although the function of the annulus in spore discharge was known prior to 1700, the details of the mechanism were not understood until the end of the last century. It was recognized that adhesion of the cell contents to the walls within annular cells is greater than cohesion. Careful observations revealed that the appearance of a bubble within the cell initiated the sudden snap of the annulus; and it was suspected that rup-

ture of the cell sap released the elastic energy of the bent annulus. In 1915 Renner[3] and Urpsrung[4] independently measured the negative pressure required for bubble formation by two methods. They obtained values of 200 to 300 atmospheres.

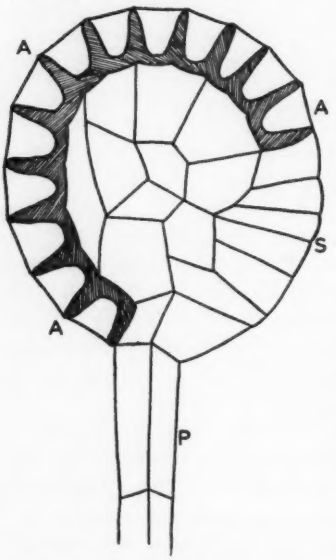

FIGURE 1

Side view of a sporangium showing location of the annulus A, the stalk or pedicel P and the stomium S. The hatched portions represent the thickened walls of the annular cells. Although spores usually may be seen through the transparent side walls of a mature sporangium, they have been omitted in this drawing.

Size of Sporangia.—The annular cell consists of thick base and radial walls and thin flexible side and outer walls. During dehiscence the base becomes recurved, the radial walls remain relatively unchanged in shape although they become reoriented, and the weak side and outer walls are pulled in. For the following analysis the cross-section of an annular cell is assumed to have the form shown in figure 2. Since the outer wall of length m is observed to be almost flat, the initial pressure inside the cell probably differs from that outside by not more than a few atmospheres. The base of length a has a radius of curvature r' and the radial walls have a height b. Just before rupture the base becomes recurved until it has a radius r. Membrane m, which is relatively inextensible, takes on a semicylindrical form provided end effects are neglected. Width l of the cell is assumed to be unaltered by the process.

Suppose the difference in pressure across membrane QR is q, directed normal to the surface as shown in figure 3. A tension T, which is constant over the entire membrane, will be set up along QR. Each element of area $l\,ds$ of the membrane is in equilibrium so that

$$T\,d\phi = q\,ds \qquad (1)$$

Since T and q are constants, Equation (1) defines a circle of radius T/q. Thus the outer wall of the annular cell becomes a cylindrical surface of length l and radius T/q. Since the membrane is semicircular in cross-section at the instant of rupture, this radius equals m/π so that the tension T has the value qm/π and makes an angle $\alpha = a/2r$ with the radial wall.

From figure 2, r' is found to be given by

$$m = 2(r' + b) \sin (a/2r') \tag{2}$$

and r by

$$m = \pi(r - b) \sin (a/2r). \tag{3}$$

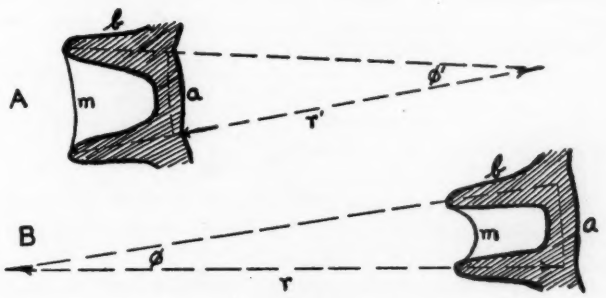

FIGURE 2

Cross-section of a single annular cell before dehiscence, *A;* at the moment of full eversion, *B*. *m* is a thin flexible membrane through which water is believed to pass during dehiscence.

The first terms in the expansions of the sine functions are sufficient for this analysis. On eliminating m from the resulting relations,

$$\frac{1}{r} = \frac{0.364}{b} - \frac{0.636}{r'}. \tag{4}$$

Values of r/b, r'/b and r'/r are entered in table 1. The product rr' has a minimum value when $r = 5.49b$ and $r' = 3.49b$.

TABLE 1

RELATION BETWEEN INITIAL AND FINAL RADII OF SPORANGIUM

r'/b	r/b	r'/r	r'/b	r/b	r'/r
1.75	∞	0.00	5.0	4.2	1.2
2.0	22.2	0.09	6.0	3.9	1.5
3.0	6.6	0.46	7.0	3.7	1.9
4.0	4.9	0.82	8.0	3.5	2.3

Since the outer wall becomes semicylindrical before bubble formation, the annulus must straighten out or recurve. The minimum value of r'/b, therefore, is 1.75 corresponding to $r = \infty$. If θ' and θ represent the initial and final angles subtended by *all* the annular cells, then

$$r'\theta' = r\theta. \tag{5}$$

The maximum value of θ is 2π, since the annulus can recurve only until its two ends meet. On the other hand, θ' usually is not less than π. For these limiting values of θ and θ' the ratio $r'/r = 2$. In table 1 this ratio is seen to occur when r'/b is slightly greater than seven. Thus the radius of a ripe sporangium is not less than 1.75, nor greater than 7 times the height of an annular cell. As shown in table 2, average values of r'/b for seven species of ferns lie well within this range.

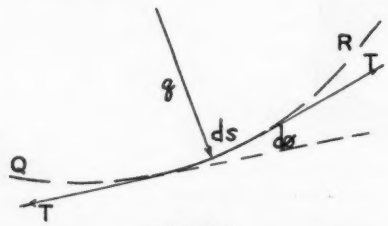

FIGURE 3

Cross-section of a portion of membrane m at the moment of full eversion showing element of length ds. The vector labeled q represents the force $ql\,ds$ and the vectors labeled T represent the force $T\,dl$.

TABLE 2

SIZES OF SPORES, SPORANGIA AND ANNULAR CELLS

SPECIES	b	a/b	c/b	r'/b*	l/b	e/b†
Cyrtomium falcatum	30 μ	0.63	0.27	3.5	2.0	1.3
Dryopteris uliginosa	31 μ	0.74	0.26	2.6	2.1	1.1
Phlebodium aureum	44 μ	0.69	0.18	3.8	1.8	1.0
Pteris cretica	38 μ	0.59	0.22	3.8	1.5	1.4
Pteris longifolia	47 μ	0.58	0.25	4.8	1.4	1.0
Nephrolepis pectinata	28 μ	0.68	0.29	4.0	1.6	0.9
Nephrolepis exaltata	29 μ	0.76	0.25	2.6	2.0	1.0
Averages	35 μ	0.67	0.25	3.6	1.8	1.1

* Usually sporangia have elliptical cross-sections. Major and minor axes were measured and r' was computed for the middle of the annulus.

† Frequently, spores are slightly ellipsoidal. Only the non-fertile spores of *Nephrolepis exaltata* (Boston fern) showed considerable variation in size.

Young's Modulus of the Annulus.—Consider a single annular cell $OPQR$ of a fully everted sporangium, as shown in figure 4. Membrane QR is a cylinder of radius T/q, as shown above, where q is the negative pressure of the cell sap on the membrane (the pressure outside is negligible). q acts uniformly over the entire inner surface of the cell. For the membrane QR, however, it may be replaced by the tension T acting along the tangent to the membrane at the juncture with the radial walls.

The moment of the forces on cell surfaces OPQ about O consists of the moment of T, the moment of q over surfaces OP and PQ and the bending moment of the elastic forces in the base OP. The effect of the weight of cells attached to PQ is very small compared with the other stresses and may be neglected. To the approximations involved here the bending moment of the base equals $EI(r + r')/rr'$, where E is Young's modulus of the base material, I is the moment of area for a transverse section of the base and r and r' are the radii of curvature before and at the instant of full eversion. The annulus is assumed to be in equilibrium just before rupture occurs, so that

$$EI(r + r')/rr' = ql\{\tfrac{1}{2}b^2 + r(r - b)(1 - \cos\phi)\} + Tl\{r \sin(\alpha - \phi) - (r - b)\sin\alpha\}. \quad (6)$$

If the transverse section of the cell base has height c, the moment of area I about the central line is $lc^3/12$. With this value of I and for small angles, equation (6) reduces to

$$E = 6qb^2rr'/c^3(r + r'). \quad (7)$$

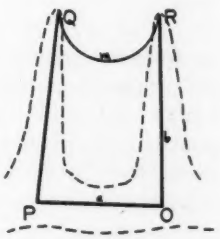

FIGURE 4

Cross-section of a single annular cell at full eversion. For the analysis in this paper the cell is assumed to have the form $OPQR$. The dotted lines indicate the actual outline of the cell walls.

With $c = b/4$, $r = 5.5b$, $r' = 3.5b$, and $q =$ 200 atmospheres, Young's modulus for the annulus comes out approximately 1.6×10^{11} dynes/cm.^{2} This value is about 25 per cent greater than that reported by Press[5] for viscose rayon yarn. Common green woods[6] have moduli ranging from 1.0 to 1.5×10^{11} dynes/cm.^{2} Since the thickened wall of the annular cell is especially spring-like, its modulus of elasticity should be somewhat greater than that for common wood fibers. The ratio of Young's modulus to the density of the annular walls is greater than the same ratio for many other solids.

Initial Speed and Range of Spores.—Since the thickened base of the annulus is a continuous structure, it may be considered a circular arc fastened to the pedicel at one end. When the sporangium is fully everted sixty odd spores are held within a cup formed by the lateral walls which remain fixed to the free end of the annulus. The total potential energy of the everted annulus is

$$W = \tfrac{1}{2}naEI(1/r + 1/r')^2, \quad (8)$$

where n represents the number of cells in the annulus and the other symbols have already been defined.

When the vapor bubble forms, the negative pressure is assumed to be entirely released; so that the annulus springs back with a snap to its original position. It is further assumed that the cup with spores is fastened to the end cell of the annulus. Even if the cup is three or four cells from the end, the initial speed and range of the spores are increased by less than 100 per cent. As the cup slips from behind it, the spore mass acquires momentum directed away from the sporangium. To a first approximation, the radius of the annular arc at the moment the spores leave is

$$R = rn/(n - 1). \tag{9}$$

This relation arises if the angle subtended by the annular arc from pedicel to spore mass, initially $(n - 1)a/r$ and finally na/R, is supposed to remain unchanged during the discharge process. The decrease in potential energy experienced by the annulus as the radius changes from r to R is

$$V = (aEI/r^2)(1 + r/r' - 1/2n). \tag{10}$$

In order to obtain an upper limit for the average speed v of spore ejection, this change in potential energy is assumed to be transformed entirely into kinetic energy of the spore mass. The kinetic energy of the moving annulus and cup and all energy losses are neglected. The kinetic energy gained by 60 spores is

$$U = 5\pi\rho e^3 v^2, \tag{11}$$

where ρ is the density and e is the diameter of each spore.

Equate U and V, eliminate EI, and solve for v. Because $r'/2n(r + r')$ is much less than unity, the average speed comes out

$$v = (aqlb^2/10\pi\rho e^3 r)^{1/2}. \tag{12}$$

On substituting average values of a, b and e from table 2, $r = 5.5b$, $\rho = 1$ g./cc. and $q = 200$ atmospheres, the speed of ejection of the spores is calculated to be 10 meters/sec.

By application of Stoke's law, the distance a spore may travel is given by

$$d = ve^2(\rho - \rho')/18\eta, \tag{13}$$

where v is the initial speed, e is the diameter and ρ the density of the spore, and η is the viscosity and ρ' the density of air.[7] $\eta = 0.00018$ poise at 20°C., $\rho = 1$ g./cc., and ρ' may be assumed negligible. Using these data and the average value of e from table 2 (nearly 40 microns) in equation (13), the range of spores is computed to be approximately 5 cm. Although this result is more than twice the observed values, the discrepancy is not unexpected. Energy losses were neglected, the mass of the spore cup was not taken into account and the problem was otherwise much idealized.

If the negative pressure q were less than 10 atmospheres or greater than

10,000 atmospheres, Young's modulus of the annular arc and the range of spores would have come out too small or too large. A sporangium can evert again and again by alternate imbibition of water and deshiscence after the spores have been expelled, even in the case of herbarium specimens more than fifteen years old.[8] This suggests that the annular cells of a spore-filled mature sporangium contain water and that this water is ruptured at the time of bubble formation. *The above computations, therefore, yield additional evidence for the belief that the tensile strength of water is around 200 atmospheres.* Haller[9] obtained 200–300 atmospheres by means of a piezo-electric device in a stream of water where cavitation occurred. Measurements by Dixon[10] and by Vincent[11] using Berthelot's method gave values as high as 150–200 atmospheres. Many experimental and theoretical values are in marked disagreement with these results; but an extensive discussion and evaluation of them is beyond the scope of this paper.

The author here expresses his appreciation for the use of the greenhouse and the helpful advice given by Professor Charles J. Lyon of the botany department at Dartmouth College. Also he is much indebted to Drs. L. J. Briggs and L. B. Tuckerman of the National Bureau of Standards for pointing out two errors in the original manuscript.

[1] Atkinson, G. F., *The Study of the Biology of Ferns by the Collodion Method*, Macmillan and Co., New York (1894), p. 68.

[2] Ingold, C. T., *Spore Discharge in Land Plants*, Oxford University Press, London (1939), p. 119.

[3] Renner, O., *Jahr. f. Wiss. Botanik*, **56**, 647 (1915).

[4] Ursprung, A., *Ber. d. Deutsche Bot. Gesell.*, **33**, 153 (1915).

[5] Press, J. J., *Jour. App. Phys.*, **14**, 224 (1943).

[6] *International Critical Tables*, Vol. II (1927), p. 6.

[7] Buller, A. H. R., *Researches on Fungi*, Vol. 1, Longmans, Green, and Co. (1909), p. 190.

[8] Atkinson, G. F., op. cit., p. 71.

[9] Haller, P. de, *Schweizerische Bauzeitung*, **101**, 260 (1933).

[10] Dixon, H. H., *Transpiration and the Ascent of Sap in Plants*, Macmillan and Co., London (1914).

[11] Vincent, R. S., *Phys. Soc. Proc.*, **53**, 126 (1941); Vincent, R. S., and Simmonds, G. H., *Phys. Soc. Proc.*, **55**, 376 (1943).

SCALE CURVES IN CONFORMAL MAPS[1]

BY EDWARD KASNER AND JOHN DE CICCO

DEPARTMENTS OF MATHEMATICS, COLUMBIA UNIVERSITY, ILLINOIS INSTITUTE OF TECHNOLOGY

Communicated May 26, 1944

1. Let a surface Σ be mapped in point-to-point fashion upon a plane π with cartesian coördinates (x, y). The scale function $\sigma = ds/dS$, which is the ratio of the corresponding elements of arc length in π and in Σ, depends, in general, not only upon the point but also upon the direction. It is independent of the direction if and only if the mapping is conformal.

We wish to present some theorems concerning the scale function σ in any general conformal mapping of a surface Σ upon a plane π, and to apply the results to the cartography of the sphere. The classic projections of Ptolemy, Mercator and Lambert appear in new light. A *scale curve* on Σ or π is the locus of a point along which the scale function σ does not vary. Therefore in the conformal case, there are ∞^1 scale curves, defined by the finite equation $\sigma(x, y) = \text{const.}$ We shall be chiefly concerned with these scale curves. In the non-conformal case, there is always a double infinity of scale curves. This will be studied in our next paper.

2. Kasner has proved that the complete system of ∞^2 isogonal trajectories of a given base family (M) of ∞^1 curves upon a surface Σ is *linear* (in the analytic sense, as distinguished from the algebraic sense) if and only if (M) is an isothermal family.[2]

This theorem is important in cartography for the following reasons. Suppose it is desired to traverse a surface Σ always cutting a given base family (M) upon Σ at a constant angle (thus defining *general loxodromes* with respect to (M) on Σ) in such a way that when Σ is mapped upon a plane π, the path described is represented in π by a straight line (for any angle). The above result states that this can be accomplished if and only if (M) is an isothermal family of curves.

If, in addition, it be desired that the base family (M) consist wholly of geodesics upon Σ, then Σ must be applicable to a surface of revolution and the family (M) must correspond to meridians. If Σ contains more than one such isothermal system (M) of geodesics, then it must contain ∞^2 such systems (M) and the surface Σ must be of constant gaussian curvature G.[3]

3. Any family of ∞^1 curves can represent the scale curves of a conformal map upon a plane π of any one of a certain class of surfaces Σ. In the present paper, we shall say that a family of curves is of the type λ if it represents the scale curves of a conformal map of a surface Σ upon a plane π such that the gaussian curvature G is constant along each of the scale curves. A family of curves $f(x, y) = \text{const.}$, is of the type λ if and only if f satisfies a certain partial differential equation of the fourth order. In that

event, it is possible to find a function $\lambda = \lambda(f)$ such that λ satisfies the partial differential equation: $\lambda_{xx} + \lambda_{yy} = \phi(\lambda)$. The logarithm of the scale function σ also satisfies a differential equation of the same form.

4. Any isothermal family is of the type λ but not every family of the type λ is isothermal. Thus the family of similar ellipses $x^2 + 2y^2 = \text{const.}$ is of the type λ but is not isothermal. We may use the term *quasi-isothermal* for the general λ type.

If the ∞^1 scale curves of a conformal map of a surface Σ upon a plane π form an isothermal system such that the gaussian curvature G is constant along each of the scale curves, then Σ is either developable or applicable upon a non-developable surface of revolution. In the former case, the scale curves may be any isothermal family (and the conformal map is of perfectly general character), but in the latter case the scale curves must be either parallel straight lines or concentric circles (and the conformal map is of special character).

5. A family of the type λ (quasi-isothermal) is parallel if and only if it consists of parallel straight lines or concentric circles. The associated surface Σ must then be either developable or applicable upon a surface of revolution.

If a developable surface Σ is mapped conformally upon a plane π with parallel curve scales, then the map is the product of an unrolling of Σ upon π by one of the transformations $Z = z^n$, $Z = \log z$, $Z = e^z$, followed by a similitude. This is entirely different from the isothermal case where the conformal map is perfectly arbitrary.

If a surface Σ of constant non-vanishing gaussian curvature is mapped conformally upon a plane π with isothermal or parallel scales, then the scales must be parallel straight lines or concentric circles. *Thus the only conformal maps of a sphere upon a plane with isothermal or parallel scales are the Mercator projection (with straight scales) and the Ptolemy stereographic and Lambert projections (with circular scales).*

6. A famous theorem of Beltrami states that if a surface Σ is mapped upon a plane π in some point-to-point fashion such that its ∞^2 geodesics are represented by straight lines in π, then Σ is of constant gaussian curvature. We shall study now the situation where not all the geodesics correspond to straight lines, but the maximum number of lines arise.

Kasner has proved that under any arbitrary point-to-point map of a surface Σ upon a plane π (or more generally, upon another surface Σ^1), there are at most 3 ∞^1 geodesics which correspond to straight lines (or geodesics on Σ^1). This is called partial geodesic representation.

In a conformal map, there are at most ∞^1 geodesics on Σ which correspond to straight lines on π (since the 2 ∞^1 minimal lines on Σ already correspond to the 2 ∞^1 minimal lines on π). If a conformal map carries exactly ∞^1 geodesics of Σ into straight lines of π, *then the scale curves of the*

conformal mapping must form a parallel curve family, and the orthogonal family is the required system of geodesics.[4]

If a surface Σ of constant gaussian curvature is conformally mapped upon a plane π such that ∞^1 geodesics of Σ are pictured by straight lines of π, then the scale curves are parallel lines or concentric circles. For the cases of a developable surface or a sphere, the maps are the ones given in Section 5.

7. The only families of ∞^1 lines or circles which are quasi-isothermal are the pencils of straight lines or circles. The associated surface Σ must be either developable or applicable to a surface of revolution. This is a large generalization of a theorem of Lagrange.

If a developable surface Σ is mapped conformally upon a plane π such that the scales are straight (or circular), the map is the product of an unrolling of Σ upon π by the transformation $Z = z^n$ (or either $Z = \log z$ or $Z = e^z$) followed by a similitude.

The only conformal map of a sphere upon a plane with straight scales is the Mercator projection. The only conformal maps of a sphere upon a plane with circular scales are the Ptolemy stereographic and Lambert projections.

8. The sphere cannot be mapped conformally on a plane so that the geodesics become straight. Geodesic circles can be mapped into circles, but not so that concentric families remain concentric (this is true even for non-conformality).

The quasi-isothermal type of family of curves (for both surface and plane) includes the Laplace, Poisson and Helmholtz-Pockels equations arising in the theory of heat conduction.[5]

[1] Presented to the American Mathematical Society, February, 1944. Some of our cartographic results have been outlined (for both the conformal and non-conformal maps) in *Science* **98**, 324–325 (1943), and in *Science News Letter*, March 25, 1944.

[2] For a recent unified discussion of this theorem, see the paper by De Cicco, "New Proofs of the Theorems of Beltrami and Kasner on Linear Families," *Bull. Am. Math. Soc.*, **49**, 407–412 (1943). The original proof appeared in *Math. Annalen*, 1904.

[3] Kasner, "Isothermal Systems of Geodesics," *Trans. Am. Math. Soc.*, **5**, 55–60 (1904).

[4] Kasner, "The Problem of Partial Geodesic Representation," *Ibid.*, **7**, 200–206 (1906).

[5] See Kasner, "Geometry of the Heat Equation," *Proc. Nat. Acad. Sci.*, **19**, 257 (1933). See. p. 261 for Fialkow's fundamental geometric property of fourth order, characterizing the quasi-isothermal type.

THE SPAN OF THE TRANSLATIONS OF A FUNCTION IN A LEBESGUE SPACE*

BY I. E. SEGAL

BALLISTIC RESEARCH LABORATORY, ABERDEEN PROVING GROUND, MD.

Communicated May 16, 1944

The refined harmonic analysis of a real or complex-valued function on the real line[1] is connected with the determination of the span,[2] in a particular space, of the translations of the function. That this span depends mainly on the zeros of the Fourier transform of the function was first indicated by Wiener.[3] He proved that, for the spaces L and L_2, the span is the entire space if and only if the Fourier transform of the function is, in some sense, non-vanishing. At the same time he raised the question of how far the analogue to this is true in a general Lebesgue space,[4] L_p. The present note is concerned with this question for the type of non-vanishing that seemed appropriate for the Fourier transform of an element of such a space, i.e., non-vanishing except on a set of Lebesgue measure zero. We show that non-vanishing of the Fourier transform is sufficient for spanning when $p > 2$, but insufficient when $1 < p < 2$. The precise result is stated in the following theorem.[5]

Let f be an element of L_p whose L_p-Fourier transform exists, where $1 < p < \infty$; and let (A) and (B) be conditions on f, as follows:

(A) The real zeros of the L_p-Fourier transform of f constitute a set of Lebesgue measure zero;

(B) The translations of f span L_p.

If $p \geq 2$, (A) implies (B). If $1 < p < 2$, (A) does not imply (B)—there exist elements of L_p for which (A) but not (B) holds; however, (B) implies (A).

For succinctness of statement, some matters of definition have been deferred; these will now be taken up.

1. The Lebesgue space L_p is either that of real or that of complex-valued functions, on the real line, in its strong topology.

2. A translation of an element, $f(\cdot)$, of L_p is a function of the form $f(x + a)$, where a is a constant.

3. In case $p > 2$ the L_p-Fourier transform of an element, f, of L_p is said to exist if f is the L_q-Fourier transform of an element of L_q, where[6] $p^{-1} + q^{-1} = 1$. (N. B.—This last relation implies $1 < q < 2$; also, for $1 < p < 2$ the L_p-Fourier transform always exists.)

Instead of giving a full proof, which would require excessive space, a condensed version is presented.[7]

LEMMA 1: *An element of L_p, $f(\cdot)$, satisfies (B) if and only if the following is true: if $g(\cdot) \in L_q$ and $\int_{-\infty}^{\infty} f(x + y)\overline{g(y)}dy = 0$ for all real values of x, then $g(\cdot) = 0$.*

By a result in the theory of Banach spaces,[8] the translations of $f(\cdot)$ span L_p if and only if no non-zero continuous linear functional vanishes on all translations. By Riesz' representation theorem,[9] every continuous linear functional on L_p, λ, has the form: $\lambda f(\cdot) = \int_{-\infty}^{\infty} f(x)\overline{g(x)}dx$, where $g(\cdot)$ is a particular element of L_q. The proof is completed by combining these facts in straightforward fashion.

At this point it is logical to divide the proof into two parts, according as $p \geq 2$ or $1 < p < 2$; the respective proofs, as well as the results, differ in general character.

Case 1: $p > 2$. This case is distinctly the simpler. The proof is indirect; suppose that $f(\cdot)$, a function satisfying the hypothesis, fulfills (A) but not (B). By Lemma 1 there exists a non-zero element of L_q, $g(\cdot)$, such that $\int_{-\infty}^{\infty} f(x+y)\overline{g(y)}dy = 0$ for all real values of x. Since $1 < q \leq 2$, the L_q-Fourier transform of $g(\cdot)$, $G(\cdot)$, exists; by hypothesis, the L_p-Fourier transform of $f(\cdot)$, $F(\cdot)$, exists. Hence the Parseval formula for Fourier transforms[10] applies, in the following manner: $\int_{-\infty}^{\infty} f(x+y)\overline{g(y)}dy = \int_{-\infty}^{\infty} e^{-ixy}F(y)\overline{G(y)}dy$. Noting that $F(y)\overline{G(y)}$ is an element of L, it follows from uniqueness theorems for Fourier transforms, and the fact that $f(\cdot)$ fulfills (A), that $g(\cdot) = 0$, a contradiction. This completes the proof, in Case 1.

Case 2: $1 < p < 2$. The proof that (A) does not imply (B) is based on two lemmas.

LEMMA 2: *Let N be a closed set of real numbers. Then there exists a function, f, that is both in L and in L_2, and whose L-Fourier transform vanishes at each point of N, and at no other real point.*

In case N is the complement of a finite open interval, there exist functions satisfying the conclusion of the lemma, and, moreover, real and non-negative; this fact follows trivially from a formula proved by Wiener.[11] For the general case, put $N = \bigcap_{k=1}^{\infty} N_k$, where N_k is the complement of some finite open interval. Let f_k be a function both in L and L_2 whose L-Fourier transform is real and non-negative and vanishes exactly on N_k. Now set $= \sum_{k=1}^{\infty} e_k f_k$, where e_k is chosen positive and so that the series is convergent both in L and L_2; e.g., take $e_k = k^{-2}\,||f_k||^{-1}$, where $||h(\cdot)|| = \int_{-\infty}^{\infty} |h(x)|dx + (\int_{-\infty}^{\infty} |h(x)|^2 dx)^{1/2}$, for an arbitrary measurable function $h(\cdot)$. It is plain that ff fulfills the condition of the lemma.

LEMMA 3: *Let q satisfy $q > 2$. Then there exists a function of bounded*

variation, $K(\cdot)$, that: (1) is purely singular and continuous, (2) has spectrum,[12] *N, of Lebesgue measure zero, (3) whose Fourier-Stieltjes transform, $g(\cdot)$, is an element of L_q.*

This lemma follows from a theorem of Salem's,[13] which states: if e is a positive number, then there exists a function of bounded variation on the interval $(0, 2\pi)$, $K(\cdot)$, that is purely singular, continuous, with spectrum of measure zero, and such that $g(n) = 0(n^{-1/2+e})$, where $g(t) = \int_0^{2\pi} e^{ilx} dK(x)$. It will be shown that this function $g(\cdot)$ is an element of L_q for every $q > \frac{2}{1-2e}$; since e can be arbitrarily small, the proof will then be complete.

Defining $n(= n(t))$ by $n - 1/2 < t < n + 1/2$, and integrating by parts, $g(t) = e^{2\pi i(t-n)} g(n) - i(t-n) \int_0^{2\pi} e^{i(t-n)x} (\int_0^x e^{inu} dK(u)) dx$. Taking absolute values, and applying Minkowski's inequality, $(\int_{-\infty}^{\infty} |g(t)|^q dt)^{1/q} \leq (\sum_{n=-\infty}^{\infty} |g(n)|^q)^{1/q} + (\int_{-1/2}^{1/2} t^q dt)^{1/q} (\sum_{n=-\infty}^{\infty} (h(n))^q)^{1/q}$, where $h(n) = \int_0^{2\pi} |\int_0^x e^{inu} dK(u)| dx$. Therefore, it is sufficient, now, to show that $\{g(n)\}$ and $\{h(n)\}$ are both in l_q, where q is an arbitrary number greater than $\frac{2}{1-2e}$ (a general element of l_q is, here, a doubly infinite sequence $s(n)$ $(n = 0, \pm 1, \ldots)$ for which $\sum_{n=-\infty}^{\infty} |s(n)|^q$ is convergent).

That $\{g(n)\} \in l_q$ is plain from Salem's theorem. To show $\{h(n)\} \in l_q$, a formal analogue to Parseval's theorem is employed, obtaining:

$$\int_0^x e^{inu} dK(u) = \frac{1}{2\pi} \sum_{m=-\infty}^{\infty} (\int_0^x e^{-imu} du)(\int_0^{2\pi} e^{i(m+n)u} dK(u));$$

this equation will now be established rigorously. Clearly, it is sufficient to show the following: if $S(\cdot)$ is a continuous function of bounded variation on $(0, 2\pi)$ such that $\{s(n)\} \in l_t$ for some $t < \infty$, where $s(n) = \int_0^{2\pi} e^{inu} dS(u)$, then $\int_0^x dS(u) = \frac{1}{2\pi} \sum_{m=-\infty}^{\infty} s(m)(\int_0^x e^{-imu} du)$. Let $f(x, r) = \sum_{n=-\infty}^{\infty} r^{|n|} e^{inx}$, where $0 < r < 1$. It is easy that:

$$(1)\ f(x, r) = \frac{1 - r^2}{1 - 2r\cos x + r^2};\quad (2)\ S(x, r) = \int_0^{2\pi} f(x - y, r) dS(x)$$

is absolutely continuous, for r constant; (3) the Fourier-Stieltjes coefficients of $S(x, r)$ are $\{r^{|n|} s(n)\}$; (4) $\frac{\partial}{\partial x} S(x, r) \in L_2(0, 2\pi)$, for r constant; (5) $\int_0^x d_u S(u, r) = \frac{1}{2\pi} \sum_{m=-\infty}^{\infty} (\int_0^x e^{-imu} du) s(m) r^{|m|}$; (6) $|(\int_0^x e^{-imu} du) s(m) r^{|m|}| \leq d(m)|s(m)|$, where $d(0) = 2\pi$ and $d(m) = 2m^{-1}$ for $m \neq 0$; (7) $\sum_{m=-\infty}^{\infty} d(m)|s(m)| < \infty$; (8) $\sum_{m=-\infty}^{\infty} (\int_0^x e^{-imu} du) s(m) r^{|m|} \to \sum_{m=-\infty}^{\infty} (\int_0^x e^{-imu} du) s(m)$, as $r \to 1$;

(9) $\int_0^x f(u - v, r)du$ is bounded for $0 < x < 2\pi$, $0 < v < 2\pi$, $0 < r < 1$, and converges to 1 or 0 as $r \to 1$ according as $x > v$ or $x < v$, respectively; (10) $\int_0^x d_u S(u, r) \to \int_0^x dS(u)$, as $r \to 1$. Combining (5), (8) and (10) yields the stated equation.

The proof that $\{h(n)\} \in l_q$ can now be completed. Taking absolute values in the expression for $\int_0^x e^{inu} dK(u)$ and integrating shows that $h(n) \leq \sum_{m=-\infty}^{\infty} d(m)|g(m + n)|$ ($d(\cdot)$ as defined in (6), preceding paragraph). It is plain that $\{g(n)\} \in l_u$ for every $u > \frac{2}{1 - 2e}$, and $\{d(n)\} \in l_v$ for every $v > 1$. Applying a theorem of Weil's[14] concerning the spaces that contain the convolution of two functions in given spaces shows that $\{h(n)\} \in l_q$.

Now the proof that (A) does not imply (B), in Case 2, will be concluded.[15] Let $g(\cdot)$, $K(\cdot)$ and N be as in Lemma 3. By Lemma 2 there exists a function, $f(\cdot)$ that is an element of both L and L_2, and whose L-Fourier transform, $F(\cdot)$, vanishes exactly on N. It is trivial that $f(\cdot)$ is an element of L_p and satisfies (A); that $f(\cdot)$ fails to satisfy (B) will now be shown. By the Fubini theorem, $\int_{-\infty}^{\infty} f(x + y)\overline{g(y)}dy = \int_{-\infty}^{\infty} e^{-ixy} F(y)d\overline{K(y)}$. Since $F(\cdot)$ vanishes on the spectrum of $K(\cdot)$, the latter integral is zero. From Lemma 1, it follows that (B) is not valid.

To prove that (B) implies (A) in Case 2, suppose this false; let $f(\cdot)$ be an element of L_p that satisfies (B), but not (A). From the latter fact it follows that there exists a measurable set of finite positive measure, S, on which the L_p-Fourier transform of $f(\cdot)$, $F(\cdot)$, vanishes. Let $G(\cdot)$ be the characteristic function of S. Plainly $G(\cdot) \in L_p$; therefore $G(\cdot)$ is the L_q-Fourier transform of an element of L_q, $g(\cdot)$. Using the Parseval formula as in the proof for Case 1, it follows that $\int_{-\infty}^{\infty} f(x + y)\overline{g(y)}dy = 0$ for all real values of x. Therefore, by Lemma 1, $f(\cdot)$ does not satisfy (B), a contradiction.[16]

* The work reported in the present note, except for the present proof of Lemma 3, was done from May to July of 1940, largely at Yale University.

[1] A complete analogue to our results holds for functions on an arbitrary locally compact Abelian group. The proof of these general results is formally the same as in the case of the real line. A full statement and proof will be given in a paper to be offered to the *Trans. Amer. Math. Soc.*

[2] By the span of a set of element we mean the least closed linear manifold containing the set.

[3] Wiener, N., "Tauberian Theorems," *Ann. Math.*, s. 2, **33**, 1–100 (1932).

[4] *Ibid.*, p. 93. Wiener stated that he suspected an analogue was probably true for $1 < p < 2$ and possibly true more generally.

[5] This theorem and its proof can both readily be extended to the case of the translations of a set of functions; the case of a single function seems fundamental, however, and we therefore postpone treating the case of a set of functions to the paper referred to in footnote 2.

[6] This relation defines q for the rest of the paper, also.

[7] A more detailed proof will be included in the paper referred to in footnote 2.

[8] Banach, S., *Théorie des opérations linéaires*, Warsaw, 1932, p. 57; "Lemme."

[9] Riesz, F., "Untersuchungen über Systeme integrierbarer Funktionen," *Math. Ann.*, **69**, 449–497 (1910); p. 475.

[10] See Titchmarsh, E. C., *Theory of Fourier Integrals*, Oxford (1937), p. 105.

[11] Wiener, N., *The Fourier Integral and Certain of Its Applications*, Cambridge, England (1933), pp. 49–50.

[12] The spectrum of a function of bounded variation consists of all points such that the total variation of the function is positive over every neighborhood of the point.

[13] Salem, R., "On Singular Monotonic Functions of the Cantor Type," *Jour. Math. and Phys.*, **21**, 69–82 (1942).

[14] Weil, A., "L'Integration dans les groupes topologiques et ses applications," *Act. Sc. et Ind.*, No. 869, Paris, p. 55 (1940).

[15] We are pleased to thank J. D. Tamarkin and A. Zygmund for suggesting a modification in the statement of Lemma 2 which results in a shortening of this part of our proof.

[16] It seems noteworthy that this argument holds for $p = 2$ also, and together with the proof for Case 1, provides a new and somewhat simpler proof of Wiener's theorem for the space L^2.

ON THE SOLUTION OF A GENERAL TRANSFORM

BY I. S. REED

DEPARTMENT OF MATHEMATICS, CALIFORNIA INSTITUTE OF TECHNOLOGY

Communicated May 15, 1944

The purpose of this paper is to give a brief extension to the solution of a Watson transform with an unsymmetric kernel. The solutions with symmetrical kernels are already well known from the work that has been done by Hardy, Watson, Titchmarsh, Goodspeed and others.

THEOREM. *If,*

(*i*) *$\alpha(u)$ and $\beta(u)$ are reciprocals of integral functions which take real values on the real axis.*

(*ii*) *$r(u)$ is an integral function such that if $u = v + iw$*

$$\left|\frac{r(u)}{\alpha(1+u)}\right| < C_1 e^{Av+B|w|}, \left|\frac{r(-u-1)}{\beta(1+u)}\right| < C_2 e^{Cv+D|w|}$$

$$0 < B < \pi, 0 < D < \pi.$$

(*iii*) *$k(s) = \alpha(s)/\beta(1-s)$, $h(s) = \beta(s)/\alpha(1-s)$ satisfy $k(s)h(1-s) = 1$ and are the Mellin transforms of $K(x)$, $H(x)$, respectively.*

(*iv*) *$k(1/2 + it)$, $\dfrac{k(1/2+it)}{1/2 - it}$ and $\dfrac{h(1/2+it)}{1/2-it}$ belong to $L^2(-\infty, \infty)$.*

Then $\sum_{n=0}^{\infty} \frac{(-1)^n r(n)x^n}{\alpha(n+1)}$ *converges for* $0 < x < e^{-A}$ *and is represented by* $f(x)$ *of* $L^2(0, \infty)$ *for all positive* x, *and* $\int_0^\infty f(x)K(xy)dx = g(y)$ *where* $g(y)$ *is of* $L^2(0, \infty)$ *and is the analytic continuation for all positive* y *of* $\sum_{n=0}^{\infty} \frac{(-1)^n r(-n-1)^n}{\beta(n+1)^n}$ *which converges for* $0 < y < e^{-C}$. *Also* $\int_0^\infty g(x)H(xy)dx = f(y)$ *for* $y > 0$. *Hence* $f(x)$ *and* $g(x)$ *are the general transforms of the unsymmetrical kernels* $K(x)$ *and* $H(x)$.

Proof. Now by Cauchy's theorem,

$$f(x) = \sum_{n=0}^{\infty} (-1)^n \frac{r(n)x^n}{\alpha(n+1)} = (1/2\pi i) \int_{a-i\infty}^{a+i\infty} \frac{\pi}{\sin \pi u} \frac{r(-u)}{\alpha(1-u)} x^{-u} du$$

when $0 < a < 1$. By condition (iv) the integral representation holds first for $0 < x < e^{-A}$ and by analytical continuation it converges uniformly in any interval $0 < x_0 \leq x \leq X$.[1] Also $f(x) = 0(x^{-a})$ for all positive x. Thus by moving the line of integration across the origin, changing the integral only by a constant, and then taking $a < -1/2$ for the lower limit of integration and $a > -1/2$ for the upper limit, we see that $\int_0^\infty \{f(x)\}^2 dx < \infty$ or is integrable in the Lebesgue sense $L^2(0, \infty)$.

It follows then by Theorem 129 of Titchmarsh's *Fourier Integral* and its extension to unsymmetrical formulae mentioned in Section 8.9 that from condition (iv) and from $f(x)$ being a function of $L^2(0, \infty)$, that the formula $g(y) = \int_0^\infty f(x)K(xy)dx$ defines almost everywhere a function $g(y)$ belonging to $L^2(0, \infty)$ and that also the reciprocal formula $f(y) = \int_0^\infty g(x)H(xy)dx$ holds.

In particular,

$$\begin{aligned}
\int_0^\infty f(x)K(xy)dx &= (1/2\pi i) \int_{a-i\infty}^{a+i\infty} \frac{\pi du}{\sin(\pi u)} \frac{r(-u)}{\alpha(1-u)} \int_0^\infty K(xu)x^{-u}dx \\
&= (1/2\pi i) \int_{a-i\infty}^{a+i\infty} \frac{\pi du}{\sin(\pi u)} \frac{r(-u)}{\alpha(1-u)} k(1-u)y^{u-1} \\
&= (1/2\pi i) \int_{a-i\infty}^{a+i\infty} \frac{\pi du}{\sin(\pi u)} \frac{r(-u)}{\beta(u)} y^{u-1} du \\
&= -(1/2\pi i) \int_{a-1-i\infty}^{a-1+i\infty} \frac{\pi dv}{\sin(\pi v)} \frac{r(-v-1)}{\beta(v+1)} y^v dv \\
&= \sum_{n=0}^{\infty} (-y)^n \frac{r(-n-1)}{\beta(n+1)} = g(y).
\end{aligned}$$

Thus the proof is complete.

Example. When $-1/2 \leq \nu < 1/2$ it is well known that if $K(x) = x^{1/2}Y_\nu(x)$ then

$$H(x) = x^{1/2}H_\nu(x)^2$$

and in this case if

$$\alpha(s) = 2^{s/2}\Gamma(1/2\nu + 1/2s + 1/4)\sec(1/2\nu - 1/2s + 3/4)\pi$$

then

$$\beta(s) = 2^{s/2}\Gamma(1/2\nu + 1/2s + 1/4)\csc(1/2s + 1/2\nu + 1/4)\pi$$

hence if $N = 1/2n + 1/2\nu + 3/4$

$$f(x) = \sum_{n=0}^{\infty} (-x/\sqrt{2})^n r(n) \cos(1/2\nu - 1/2n + 1/4)\pi/\Gamma(N)$$

$$g(x) = \sum_{n=0}^{\infty} (-x/\sqrt{2})^n r(-n-1) \sin(1/2\nu + 1/2n + 3/4)\pi/\Gamma(N).$$

If, moreover, $r(n) = \sec(1/2\nu - 1/2n + 1/4)$, then $r(-n-1) = \sec(1/2\nu + 1/2n + 3/4)\pi$ and so

$$g(x) = \sum_{n=0}^{\infty}(-x/\sqrt{2})^n \tan(N\pi)/\Gamma(N) =$$

$$\lambda(x) \tan(1/2\nu + 3/4)\pi + \mu(x) \cot(1/2\nu + 3/4)\pi$$

where

$$\lambda(x) = \sum(1/2x^2)^n/\Gamma(1/2\nu + n + 3/4),$$

$$\mu(x) = \sum_{n=0}^{\infty} (1/2x^2)^{n+1/2}/\Gamma(1/2\nu + n + 3/4).$$

Also

$$f(x) = \sum_{n=0}^{\infty} (-x/\sqrt{2})^n/\Gamma(N) = \lambda(x) - \mu(x).$$

Again, if

$$r(-n-1) = \csc(N\pi), \text{ then } r(n) = \csc(1/2\nu - 1/2n + 1/4)\pi$$

and

$$g(x) = \lambda(x) - \mu(x), f(x) = \lambda(x) \cot(1/2\nu + 1/4)\pi + \mu(x) \tan(1/2\nu + 1/4)\pi.$$

Also it is known that[3]

$$\lambda(y) - \mu(y) = \int_0^\infty \{\lambda(x) - \mu(x)\}(xy)^{1/2}J_\nu(xy)dx$$

so we obtain the identity

$$\begin{aligned}\lambda(y) - \mu(y) &= \int_0^\infty \{\lambda(x) - \mu(x)\}(xy)^{1/2} J_\nu(xy)dx \\ &= -\int_0^\infty [\lambda(x)\cot(1/2\nu + 1/4)\pi + \mu(x)\tan(1/2\nu + 1/4)\pi] \\ &\qquad (xy)^{1/2} H_\nu(xy)dx \\ &= \int_0^\infty [\lambda(x)\cot(1/2\nu + 1/4)\pi + \mu(x)\tan(1/2\nu + 1/4)\pi] \\ &\qquad (xy)^{1/2} Y_\nu(xy)dx\end{aligned}$$

also

$$\int_0^\infty [\lambda(x)\cot(1/2\nu + 1/4)\pi + \mu(x)\tan(1/2\nu + 1/4)\pi](xy)^{1/2}[H_\nu(xy) + Y_\nu(xy)]dx = 0.$$

[1] Hardy, G. H., "Ramanujan and the Theory of Fourier Transforms," *Quart. Jour. Math.* (Oxford series), **8**, 245–254 (1937).

[2] Titchmarsh, E. C., *Theory of Fourier Integrals*, p. 215 (1937), Oxford.

[3] Hardy, G. H., *Ramanujan*, p. 208.